



Effects of male ageing on sperm motility parameters in *Luciobarbus callensis* (Cyprinidae) from the Agrioun River, Algeria

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Abstract

Sperm quality directly affects reproductive success and population sustainability in native North African freshwater fish species such as *Luciobarbus callensis*, yet age-related effects remain underexplored under natural conditions. This study aimed to examine how fish age influences sperm quality parameters to identify optimal reproductive ages for conservation and aquaculture strategies in North African river systems. Sperm samples from *L. callensis* were examined microscopically for sperm volume (SV), sperm motility duration (SMD), and sperm concentration (SC), and analyzed with the Sperm Class Analyzer (SCA) for velocity straight line (VSL), velocity average path (VAP), velocity curvilinear (VCL), beat cross frequency (BCF), amplitude of lateral head displacement (ALH), straightness (STR), linearity (LIN), and wobble (WOB). Fish age was determined by counting translucent zones on sagittal otoliths examined under SEM (left and right otoliths), following a standard protocol in which each opaque-translucent pair represents one year (+), with an additional 0–8 months. Peaks in SMD, SC, VSL, VAP, BCF, STR, LIN and WOB occurred at age 2⁺ years, with values of 53.28 ± 0.82 s, $(9.49 \pm 0.06) \times 10^9$ spz/mL, 19.17 ± 1.41 μ m/s, 27.32 ± 1.48 μ m/s, 7.65 ± 0.24 Hz, $0.63 \pm 0.021\%$, $0.52 \pm 0.022\%$, and $0.77 \pm 0.01\%$, respectively. Sperm volume peaked at 4⁺ years (1360.45 ± 5.35 μ L), whereas VCL and ALH reached maximum values at 3⁺ years (34.36 ± 0.75 μ m/s; 1.20 ± 0.027 μ m). SV and ALH exhibited an inverse relationship with BCF, while a positive correlation between age and SV was observed ($r=0.40$), indicating that SV increased with age. Sperm quality in *Luciobarbus callensis* is defined by specific sperm parameters, but is also significantly influenced by fish age.

Keywords Algeria *Luciobarbus callensis* male age sperm quality

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Introduction

The Algerian barbel, *Luciobarbus callensis* (Teleostei: Cyprinidae), is a freshwater fish species native to North Africa (Kara 2012). In Algeria, several recent studies have shown that the abundance of freshwater fish species is decreasing, especially *Luciobarbus callensis* in natural conditions (Aberkane et al. 2018; Khebbache et al. 2017). In the study of fish, the quality of male gametes is primarily assessed through several key parameters; the duration of sperm motility, the concentration and volume of sperm, the morphology of sperm cells, their fertilization potential, and the composition and osmolality of the seminal plasma (Aberkane and Iguer-ouada 2016; Billard et al. 1995; Linhart et al. 2000; Nichols et al. 2021; Rurangwa et al. 2004). Likewise, many studies have demonstrated that sperm motility parameters, specifically velocity straight line (VSL), velocity average path (VAP), and velocity

curvilinear (VCL), as well as straightness (STR), linearity (LIN), beat cross frequency (BCF), and amplitude of lateral head displacement (ALH), are effective indicators of fertility potential (Kime et al. 2001). These metrics offer detailed insights into sperm motility characteristics that closely correlate with fertilization success, making them valuable predictors in reproductive assessments (Oliveira et al. 2013; Viveiros et al. 2010). Sperm quality parameters are influenced by both intrinsic factors (age, genetics) and extrinsic factors (pH, temperature, ions, osmolality, pollutants). Sub-optimal pH, elevated temperatures, ionic imbalances, and osmolality variations impair sperm motility and velocity in cyprinids (Alavi and Cosson 2005, 2006; Lahnsteiner and Mansour 2012; Merino et al. 2023), while heavy metal pollution reduces sperm concentration in freshwater fish (Kime 1995) and induces oxidative stress and hormonal disruption in mammals (Anyachor et al. 2025; Eddie-Amadi et al. 2025). Hypoxia impairs mitochondrial function, thereby reducing motility (Lahnsteiner et al. 1999), and glyphosate significantly diminishes VSL, VAP, and VCL (Özgür 2025). These environmental stressors interact synergistically with intrinsic factors such as male age (Aliniya et al. 2013; Fallah Shamsi and Khara 2015; Liley et al. 2002); older fish exhibit declining motility even under optimal water conditions, whereas juveniles demonstrate greater pollution resilience (Rurangwa et al. 2004). This multifactorial interplay necessitates the evaluation of age-dependent sperm quality under natural conditions, where cumulative environmental exposures occur throughout the fish life cycle. Previous studies have focused on *Luciobarbus callensis*, including systematics (Doadrio et al. 2015; Machordom and Doadrio 2001; Machordom et al. 1995), genetics (Brahimi et al. 2016, 2017), ecology (Berrebi et al. 1995), biology (Berrouk et al. 2020), biochemistry (Sila et al. 2012), parasites (Abbaci et al. 2023), bioindicators (Habla et al. 2017), reproduction (Aberkane et al. 2018), salinity tolerance (Allalgua et al. 2021), diet and growth (Salhi et al. 2021) and pollution (Khebbache et al. 2017). Nevertheless, to the best of our knowledge, no studies have yet investigated sperm quality at different ages in *Luciobarbus callensis* under natural conditions. Thus, it is important to determine whether age differences affect sperm motility parameters. Moreover, knowledge of sperm quality in *L. callensis* at various ages is fundamental for the implementation of reintroduction and conservation programs in natural environments.

Materials and methods

Handling of fish and collection of gametes

Barbels (*Luciobarbus callensis*, Cyprinidae) were collected from the Agrioun River during the spawning season between March 2022 and March 2023 (Fig. 1), when water temperature ranged from 13 to 25 °C and day length varied between 12 h 30 min and 14 h 30 min (Table S1). Specimens were collected using a fishing rod in combination with a lift net (2 cm mesh size). A total of 159 individuals were collected and classified into four age groups: 2⁺ ($n=50$), 3⁺ ($n=45$), 4⁺ ($n=38$), and 5⁺ ($n=26$). All individuals from each age class were included in the subsequent analyses according to the experimental design. Body weights ranged from 3.85 to 327.70 g, and total lengths from 7.50 to 33.30 cm. The fish were transported alive to the laboratory. The genital papilla was carefully dried and cleaned using a paper towel to prevent water contamination that could prematurely activate spermatozoa. Subsequently, semen was collected by exerting gentle pressure on the abdomen. Any samples contaminated with feces or urine were excluded from the study (Gallego et al. 2013).

Sperm analysis

Sperm samples were diluted 1:1000 (v: v) (1 µL of milt mixed with 999 µL activator) and simultaneously activated using water collected from the Agrioun River at Boulzazene (S1) and Souk El Tenine (S2) stations. SMD was quantified chronometrically; the cessation of motility was recorded once the proportion of active spermatozoa fell below a 5% threshold (Tuset et al. 2008). Sperm concentration (SC) was assessed microscopically using a haemocytometer; the minimum detectable concentration was 1×10^6 sperm/mL. For the 5⁺ age class, SC was consistently below this detection limit, preventing accurate quantification. The SCA system (ver. 4.0, 2014, Microptic S.L.) was utilized to analyze VSL, VAP, VCL, BCF, ALH, STR, LIN, and WOB.

Otolith analysis

Sagittal otoliths (left and right) were removed from each fish and prepared for age determination according to a standard protocol (David and Isely 1994). All otoliths were examined under reflected light using scanning electron microscopy (SEM) (Fig. 2a). Annual growth was interpreted from the succession of opaque and translucent zones, and the determination of fish age was conducted by counting the total number of translucent zones observed on the otoliths (Fig. 2b). A narrow translucent band is deposited in winter (November to January), whereas a wider opaque band forms

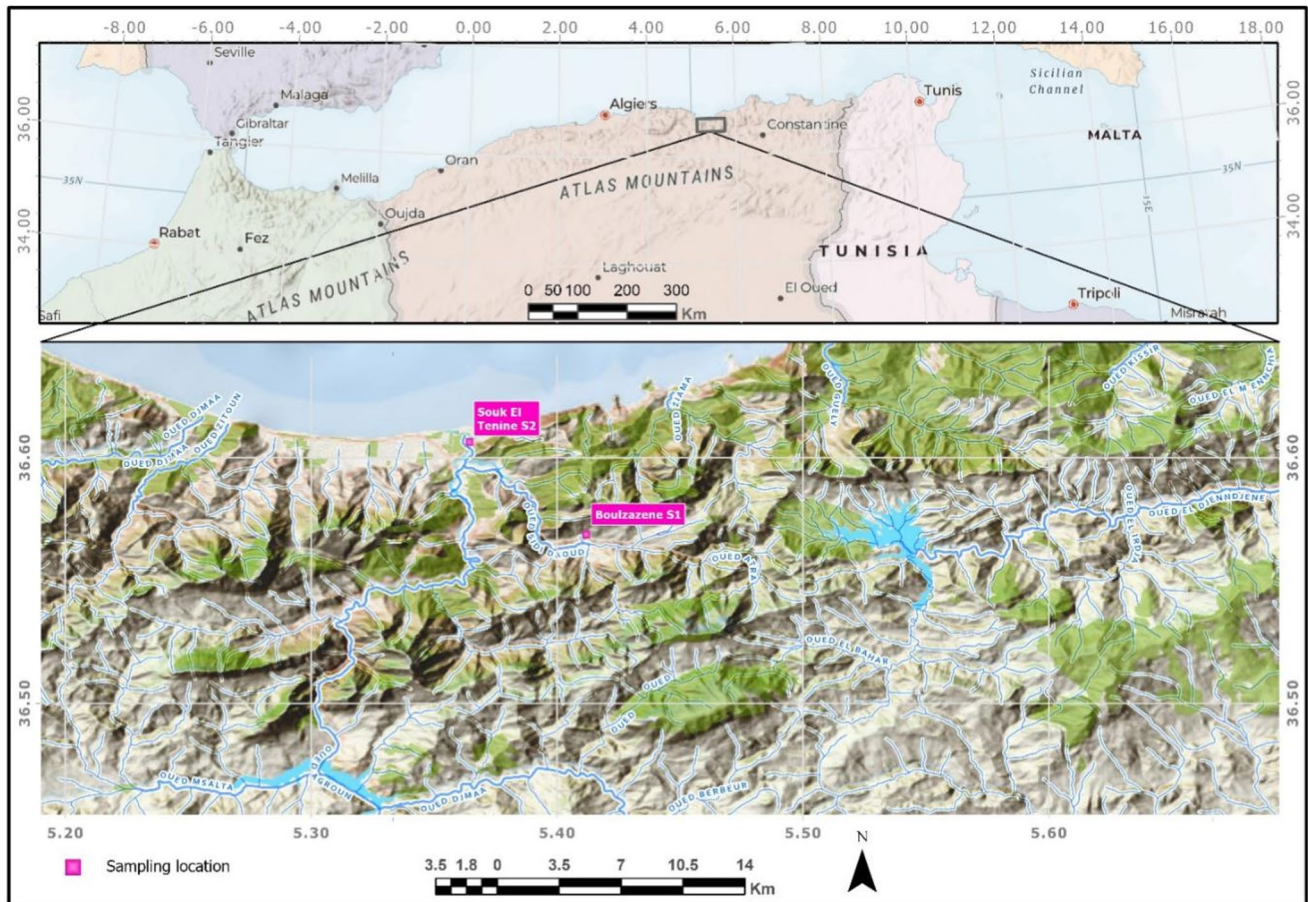


Fig. 1 Location map of the Agrioun River (S₁: Boulzazene station; S₂: Souk El Tenine station)

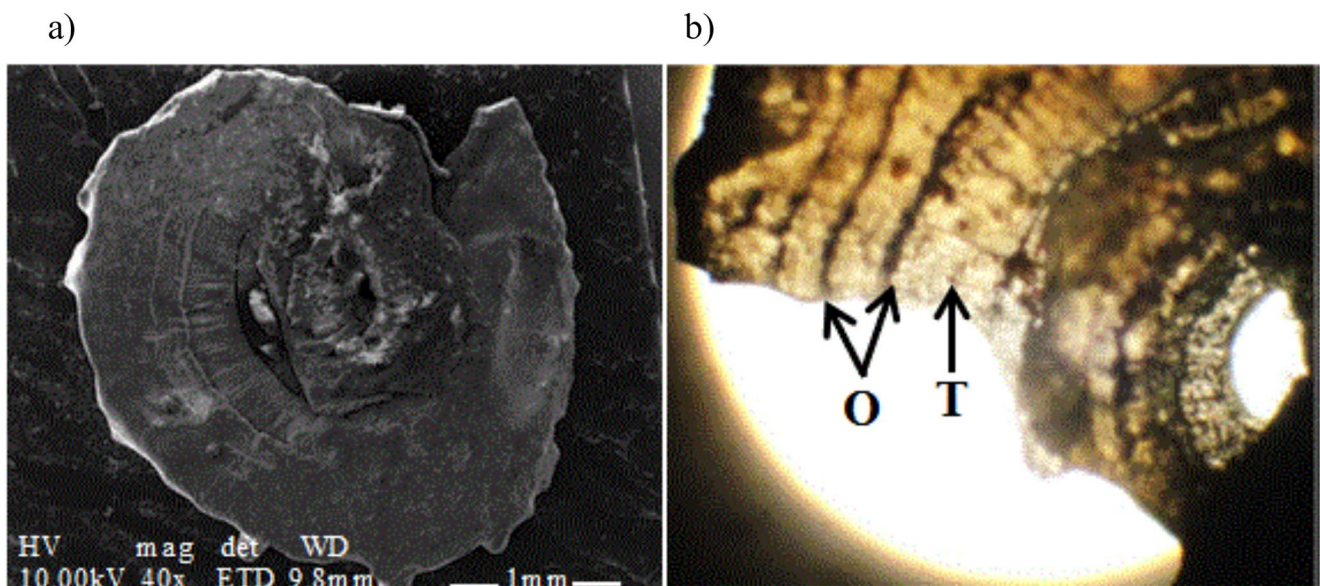


Fig. 2 (a) Observation of a sagittal otolith from a male *Luciobabrus callensis* using scanning electron microscopy (SEM). (b) Microscopic observation (x10) of a sagittal otolith from a male *Luciobabrus cal-*

lensis (TL= 23 cm) after treatment, showing the opaque (O) and translucent (T) zones under transmitted light

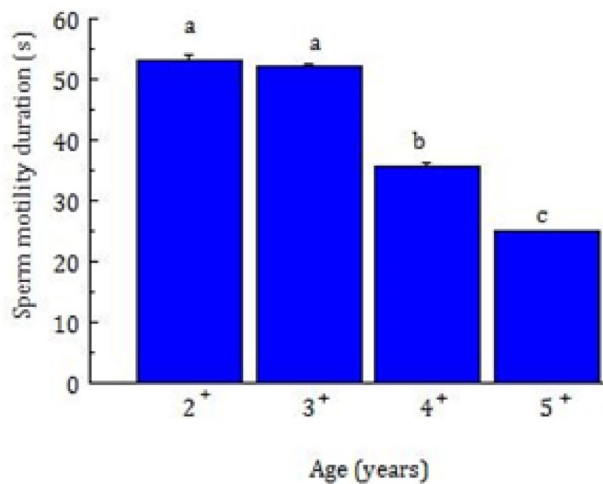


Fig. 3 Relationship between sperm motility duration (SMD, s) of *Luciobarbus callensis* spermatozoa and age (years). (+)=0 to 8 months old. The data are reported as ($M \pm SE$, $n=159$)

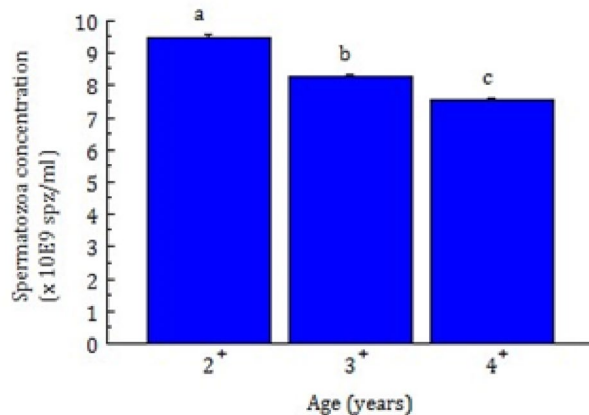


Fig. 4 Relationship between spermatozoa concentration (SC, $\times 10^9$ spz/ml) of *Luciobarbus callensis* and age (years). (+)=0 to 8 months old. The data are reported as ($M \pm SE$, $n=159$)

during the remainder of the year; together, one translucent and one opaque band correspond to a single year of growth. Accordingly, a plus sign (+) was added to the estimated age (in years) to indicate an additional 0 to 8 months.

Statistical analysis

Statistical analyses were performed using StatView 5.0 software (Abacus). Experiments were conducted in triplicate ($n \geq 3$) at minimum to ensure reliability and reproducibility. Data are expressed as means $\pm$ standard error (SE). Normality was confirmed by the Shapiro-Wilk test, and homogeneity of variances by Levene's test ($p > 0.05$ in both cases). Effects of male age on *Luciobarbus callensis* semen parameters were analyzed using a one-way ANOVA, followed by Tukey's HSD post hoc test for multiple comparisons

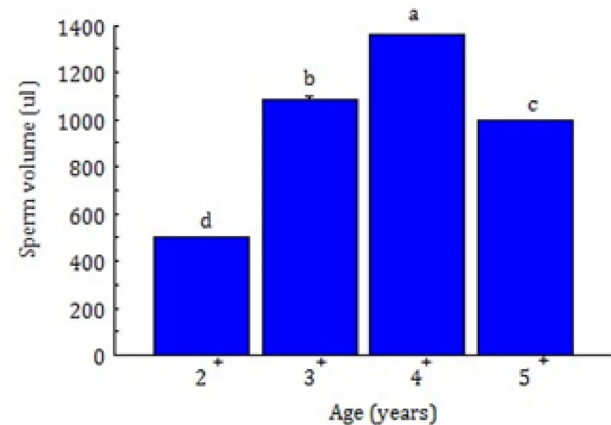


Fig. 5 Relationship between sperm volume (SV, μL) of *Luciobarbus callensis* and age (years). (+)=0 to 8 months old. The data are reported as ($M \pm SE$, $n=159$)

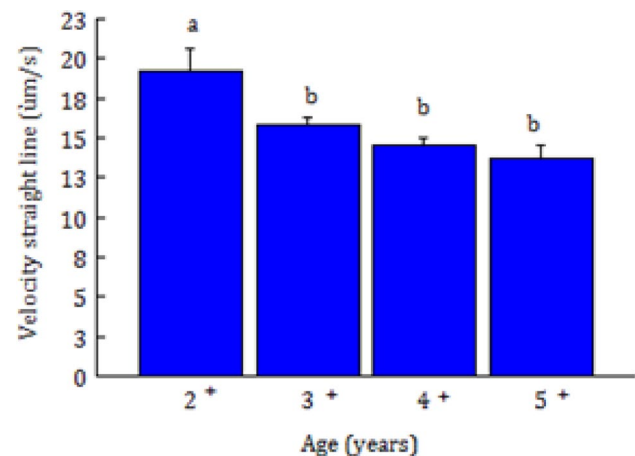


Fig. 6 Relationship between straight line velocity (VSL, $\mu\text{m/s}$) of *Luciobarbus callensis* spermatozoa and age (years). (+)=0 to 8 months old. Values are presented as mean $\pm$ standard error ($n=159$). The data are reported as ($M \pm SE$, $n=159$)

($\alpha=0.05$). No significant differences were detected between sites S1 and S2 (one-way ANOVA, $F=0.90$, $p=0.10 > 0.05$).

Results

Figure 3 shows SMD according to male age. SMD was highest in 2+ year fish (53.28 ± 0.82 s) and lowest in 5+ year fish (25.0 ± 0.0 s). Spermatozoa concentration (SC) decreased significantly with age, from $(9.49 \pm 0.06) \times 10^9$ spz/mL in 2+ fish to $(7.54 \pm 0.05) \times 10^9$ spz/mL in 4+ fish (Fig. 4). Sperm volume (SV) increased from 500 ± 0.00 μL at 2+ years to 1360.45 ± 5.35 μL at 4+ years, then decreased to 500 ± 0.00 μL at 5+ years (Fig. 5, $p < 0.05$).

SCA motility parameters, particularly VSL (Fig. 6), VAP (Fig. 7), and VCL (Fig. 8) decreased from 2+ to 5+ years: VSL

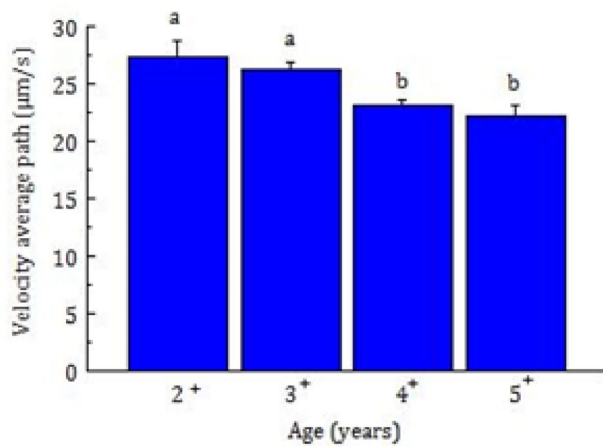


Fig. 7 Relationship between average path velocity (VAP, $\mu\text{m/s}$) of *Luciobarbus callensis* spermatozoa and age (years). (+)=0 to 8 months old. The data are reported as ($M \pm SE$, $n=159$)

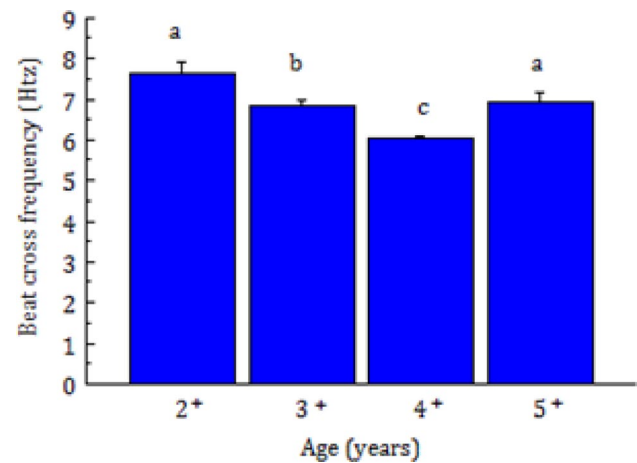


Fig. 9 Relationship between beat cross frequency (BCF, Hz) of *Luciobarbus callensis* spermatozoa and age (years). (+)=0 to 8 months old. The data are reported as ($M \pm SE$, $n=159$)

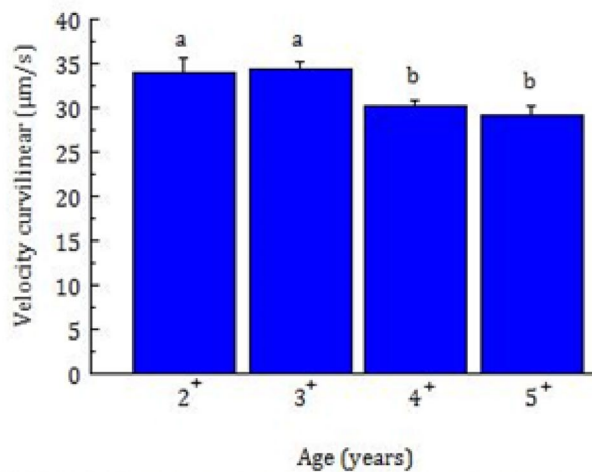


Fig. 8 Relationship between curvilinear velocity (VCL, $\mu\text{m/s}$) of *Luciobarbus callensis* spermatozoa and age (years). (+)=0 to 8 months old. The data are reported as ($M \pm SE$, $n=159$)

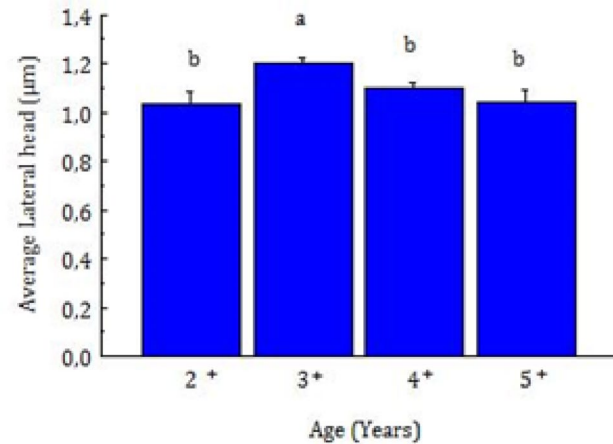


Fig. 10 Relationship between amplitude of lateral head displacement (ALH, μm) of *Luciobarbus callensis* spermatozoa and age (years). (+)=0 to 8 months old. The data are reported as ($M \pm SE$, $n=159$)

was $19.17 \pm 1.41 \mu\text{m/s}$ at 2+ years and $13.67 \pm 0.83 \mu\text{m/s}$ at 5+ years, VAP was $27.32 \pm 1.48 \mu\text{m/s}$ and $22.16 \pm 1.00 \mu\text{m/s}$, and VCL was $34.00 \pm 1.58 \mu\text{m/s}$ and $29.07 \pm 1.17 \mu\text{m/s}$, respectively. Similar trends were observed for SMD, SC, VSL, VAP, and VCL in 3+ and 4+ year-old fish (Table 1). BCF (Fig. 9) varied with age and showed opposite trends to ALH (Fig. 10) and SV (Fig. 5). The highest BCF values were recorded at 2+ and 5+ years ($7.65 \pm 0.24 \text{ Hz}$ and $6.95 \pm 0.22 \text{ Hz}$), whereas ALH reached its highest values at 3+ and 4+ years ($1.20 \pm 0.02 \mu\text{m}$ and $1.10 \pm 0.01 \mu\text{m}$, respectively). STR, LIN, and WOB also differed significantly with male age. The highest values of these parameters were

observed at 2+ years: $0.63 \pm 0.02\%$ for STR, $0.52 \pm 0.02\%$ for LIN, and $0.77 \pm 0.01\%$ for WOB.

Discussion

Age-related variation in male reproductive traits is widespread among animal taxa, including teleost fishes (Casselman et al. 2006; Kurta et al. 2023; Risopatrón et al. 2018), invertebrates (Kupriyanova and Havenhand 2002), humans (Fréour et al. 2012; Kidd et al. 2001; Reinhardt 2007), and birds (Moller et al. 2009). The main result of the present study in *Luciobarbus callensis* is the existence of a clear

Table 1 Age-related variations in sperm motility parameters of *Luciobarbus callensis*

Age (Years)	SMD (s)	SC ($\times 10^9$ spz/mL)	VSL ($\mu\text{m/s}$)	VAP ($\mu\text{m/s}$)	VCL ($\mu\text{m/s}$)
3+	$52.08 \pm 0.39 \text{ s}$	8.26 ± 0.05	$15.77 \pm 0.51 \mu\text{m/s}$	$26.18 \pm 0.63 \mu\text{m/s}$	$34.36 \pm 0.75 \mu\text{m/s}$
4+	$35.69 \pm 0.42 \text{ s}$	7.54 ± 0.05	$14.57 \pm 0.36 \mu\text{m/s}$	$23.12 \pm 0.44 \mu\text{m/s}$	$30.31 \pm 0.52 \mu\text{m/s}$

ontogenetic shift in reproductive investment between age classes, rather than a simple and uniform decline in ejaculate quality. Younger males (2^+ years) concentrate on sperm quality, showing longer motility duration, swimming velocities (VSL, VAP, VCL) and progressive kinematics (STR, LIN), possibly due to limited testicular volume and energetic reserves. Conversely, prime-aged (4^+ years) individuals switch strategy to maximize total sperm quantity and ejaculate volume, offsetting moderate reductions in single-cell swimming performance. Finally, older males (5^+ years) exhibit significant functional impairment in all ejaculate traits, indicating clear reproductive senescence.

Such a physiological trade-off between sperm quality and quantity reflects age-specific life history investments. In young, smaller males, high sperm velocity and swimming linearity are crucial for competing in sperm competition scenarios where gonadal output is physically constrained. By contrast, older, larger males benefit from a high seminal volume and total output to fill larger spawning areas or to ensure gamete encounter rates, even if individual spermatozoa exhibit a reduced flagellar kinetics. Similar trade-offs between sperm velocity and ejaculate volume across age classes have also been documented in guppy (*Poecilia reticulata*) and zebrafish (*Danio rerio*) (Evans et al. 2002; Gasparini et al. 2010; Kanuga et al. 2011), while other species such as bluegill (*Lepomis macrochirus*) or rainbow trout (*Oncorhynchus mykiss*) exhibit opposite or age-independent patterns (Casselman and Montgomerie 2004; Liley et al. 2002), thus indicating interspecific variation in reproductive strategies.

The physiological mechanisms responsible for the observed decrease in sperm velocity (VSL, VAP, VCL) and flagellar oscillation parameters (BCF, ALH) in older classes of *L. callensis* are closely related to cellular aging and oxidative degradation. During aging, the main enzymatic antioxidant defenses such as superoxide dismutase (SOD), catalase (CAT) and glutathione (GSH) progressively decline in teleost males, leading to an increased generation of reactive oxygen species (ROS) in the seminal plasma (Lahnsteiner et al. 2010; Aitken et al. 2014; Shaliutina et al. 2015). The high content of polyunsaturated fatty acids in teleost sperm membranes leads to extensive lipid peroxidation following the accumulation of ROS which alters membrane fluidity and receptor integrity (Aitken et al. 2014). Furthermore, mitochondrial dysfunction in aging spermatozoa impairs the ATP production necessary for flagellar propulsion, thus directly explaining the reduced curvilinear (VCL) and straight-line velocities (VSL) and non-progressive vibrational swimming in older age classes (Espinosa-Araujo et al. 2025). In addition to motility mechanics, continuous oxidative stress results in sperm DNA fragmentation and epigenetic modifications, both of which are considerable

threats to fertilization efficiency and post-zygotic embryo survival (Rurangwa et al. 2004; Kurta et al. 2023).

The results have important ecological and conservation implications for the endemic freshwater species *Luciobarbus callensis*, which is subjected to increasing anthropogenic pressures and overfishing in the North African river basins. In terms of population dynamics, the 2^+ and 4^+ age classes play different but complementary functional roles in spawning events, with young males providing highly competitive, highly motile gametes, and middle-aged males providing the bulk of seminal fluid needed to fertilize large egg batches. Selective removal of younger classes reduces sperm competition efficiency, whereas overharvesting of middle-aged and larger cohorts can severely deplete ejaculate volume across spawning grounds. Therefore, artificial breeding and captive broodstock management programs for *L. callensis* should consciously maintain a balanced multi-age population structure and specifically a mix of 2^+ and 4^+ males rather than exclusively single-age groups. The inclusion of such age-dependent reproductive parameters in stock assessment models will be essential to setting effective harvesting thresholds, rehabilitating wild populations and maintaining long-term genetic diversity under environmental stress.

Conclusion

Overall, this study provides the first comprehensive insights into the age-related dynamics of sperm quality in *Luciobarbus callensis* under natural conditions. We found a clear ontogenetic trade-off between sperm quality and quantity. Young males (2^+ years) invest in cellular performance producing the optimal sperm motility duration, concentration and velocity of spermatozoa. Mature adults reach a quantitative reproductive peak at 4 years old, maximizing total sperm volume. This substantial investment drops precipitously in individuals older than 5 years, representing a critical physiological threshold in the species' life history. The difference between *L. callensis* and other teleosts highlights that the pattern of reproductive aging is highly species-specific, probably due to different mechanisms of spermatogenesis or structural differences of spermatozoa. The recognition of this 4^+ reproductive peak and its senescent drop provides, in the end, key biological cues for freshwater fisheries management and conservation in North African ecosystems, emphasizing the importance of preserving mature age classes for sustainable population recruitment. More research is needed to understand the cellular mechanisms behind this decline and how it directly affects fertilization success in the wild.

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Data availability Data is contained within the article or supplementary information. Further inquiries can be directed to the corresponding author.

Declarations

Competing interests The authors declare no conflicts of interest.

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